

Pachylemur remains were first described in 1895 by French zoologist Henri Filhol and were originally included in the genus *Lemur*, along with the ring-tailed lemur and other close relatives currently classified within the family Lemuridae. In 1948, French paleontologist Charles Lamberton placed the species in the subgenus *Pachylemur*, which was recognized as a genus by 1979. However, due to earlier uses of the name *Pachylemur*, the priority of an alternative genus name proposed by Guillaume Grandidier in 1905, and errors in Lamberton's 1948 description of the genus, the availability of the name under the rules of zoological nomenclature was considered questionable. In 2011, a petition was filed with the International Commission on Zoological Nomenclature to preserve the name.

Synonyms:

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- *Lemur insignis* Filhol, 1895
- *Lemur intermedius* Filhol, 1895

- †*P. jullyi* (G. Grandidier, 1899)

Synonyms:

- *Palaeochirogalus jullyi* G. Grandidier, 1899
- *Lemur jullyi* Standing, 1904
- *Lemur maxiensis* Standing, 1904
- *Lemur majori* Standing, 1908



Subfossil sites for *Pachylemur*^[1]

red = *P. insignis*; **blue** = *P. jullyi*;
black = *P. sp.* (uncertain)

Synonyms

- *Palaeochirogalus* G. Grandidier, 1899

Evolutionary history

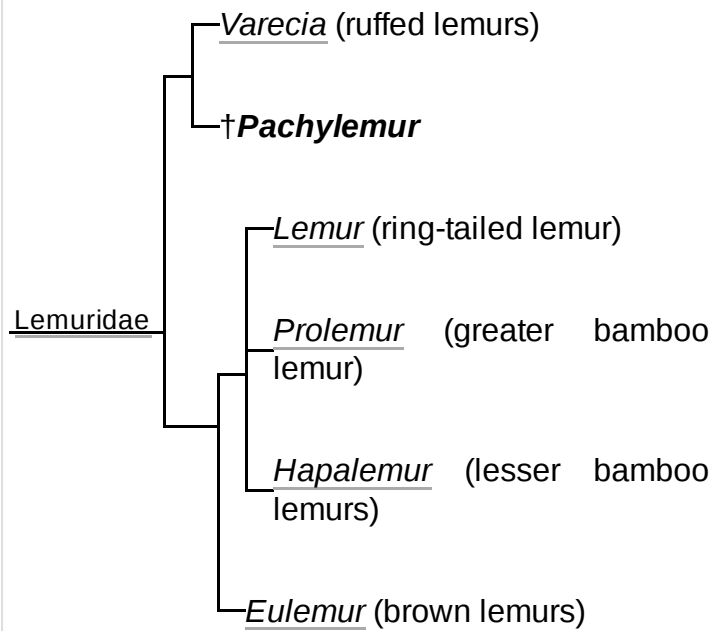
Pachylemur was similar to but significantly larger and more robust than living ruffed lemurs (genus *Varecia*).^{[2][3]} In addition to their general morphology, studies of their teeth (dental anatomy) also suggest a close relation.^[4] In 1953, William Charles Osman Hill noted that the skull of both *P. insignis* and *P. jullyi* (then called *Lemur insignis* and *L. jullyi*) resembled that of ruffed lemurs more so than the rest of the lemurs classified in the genus *Lemur* at that time.^[5]

Because of the similarities, *Pachylemur* is sometimes referred to as a giant ruffed lemur.^[6] In addition to the morphological similarities, molecular studies also support a close relationship.^[4] Based on studies of their DNA, *Pachylemur* and ruffed lemurs form the sister group relative to the rest of the lemurs in the family Lemuridae. This sister group itself forms a sister group with the clade (related group) containing brown lemurs (*Eulemur*), the ring-tailed lemur (*Lemur*), the greater bamboo lemur (*Prolemur*), and the lesser bamboo lemurs (*Hapalemur*).^[1]

Taxonomic classification

French zoologist Henri Filhol was the first to scientifically describe a species of *Pachylemur*; he named *Lemur insignis* and *Lemur intermedius* in 1895 on the basis of a few subfossil bones.^[7] Descriptions of other species now placed in *Pachylemur* quickly followed. In 1899, Guillaume Grandidier named a new genus and species, *Palaeochirogalus jullyi*,^[a] on the basis of two teeth from Antsirabe, central Madagascar, which he thought similar to dwarf lemurs (*Cheirogaleus*).^[8] In 1903, Grafton Elliot Smith placed this species in the genus *Lemur* (as *Lemur jullyi*),^[9] and in 1905, Grandidier himself considered the species a synonym of *Lemur insignis*.^[10]

Phylogeny of family Lemuridae^{[5][11][12]}



Ruffed lemurs are the closest living relatives of *Pachylemur*, and both form a sister group to the other lemurids.

Meanwhile, in 1904, Herbert F. Standing had named a different species using the same name, *Lemur jullyi*,^[13] and named another species *Lemur maziensis*.^[14] He noted similarities between this group and the ruffed lemurs, then considered a single species, *Lemur varius*.^[15] In 1908, Standing named another species in the group, *Lemur majori*,^[16] and included his *Lemur maziensis* in *L. jullyi*.^[17] The name *Pachylemur* was introduced for these animals in 1948 by Charles Lamberton, who grouped *Lemur insignis*, *Lemur majori*, and *Lemur jullyi* in a subgenus of the genus *Lemur*.^[18]

Since 1979, *Pachylemur* has generally been regarded as a distinct genus, but some classifications include the genus in *Lemur* or the ruffed lemur genus *Varecia*.^{[19][20]} In a 1982 review, Ian Tattersall recognized two species, *Lemur insignis* and *Lemur jullyi*. He did not regard *Pachylemur* as a distinct genus or even subgenus. As Tattersall noted, *Lemur jullyi*

Standing, 1904, is preoccupied by *Palaeochirogalus jullyi* Grandidier, 1899, and thus invalid. However, both names are based on material from the central plateau of Madagascar and Tattersall therefore presumed that they belong to the same species, which he could continue to call *Lemur jullyi*.^[21] Recent classifications recognize *Pachylemur* as a valid genus with two species—*P. insignis* (Filhol, 1895) and *P. jullyi* (Grandidier, 1899)—but express doubt about the distinction between the two species.^{[4][19]}

There are several nomenclatural problems with the current use of the name *Pachylemur*.^[22] First, Filhol had himself used the name *Pachylemur* in 1874 for a group of primitive primates, including *Adapis*, that he considered intermediate between pachyderms and lemurs.^[23] Several other authors mentioned this name in the 19th and early 20th centuries, but it is questionable that any rendered the name available under the rules of zoological nomenclature.^[24] Still, this name potentially renders *Pachylemur* Lamberton, 1948, invalid under the Principle of Homonymy.^[19] In addition, the generic name *Palaeochirogalus* Grandidier, 1899, predates *Pachylemur* Lamberton, 1948, by half a century and thus takes precedence under the Principle of Priority, and *Pachylemur* Lamberton is itself unavailable because Lamberton failed to select a type species.^[25] To conserve the name *Pachylemur*, Jelle Zijlstra, Colin Groves, and Alex Dunkel submitted a petition to the International Commission on Zoological Nomenclature in 2011.^[26] The petition asks the Commission to suppress the names *Pachylemur* Filhol, 1874, *Pachylemur* Palmer, 1904 (based on Filhol's name), and *Palaeochirogalus* Grandidier, 1899, and to make *Pachylemur* Lamberton, 1948, retroactively available with *Lemur insignis* as its type species.^[27]

Anatomy and physiology

Pachylemur resembled the living ruffed lemurs but was three or four times larger, with an estimated body mass of 10 kg (22 lb) for *P. insignis* and 13 kg (29 lb) for the larger *P. jullyi*.^{[4][28]} In addition, the skeleton is more robust.^[4]

The dental formula is $\frac{2.1.3.3}{2.1.3.3}$, as in all lemurids. The toothcomb—a comblike structure formed by the lower front teeth, characteristic of lemurs and lorisoids—is similar to that of other lemurids. The two halves of the mandible (lower jaw) do not fuse at the mandibular symphysis.^[4] However, there are some differences in tooth



The skull and teeth of *Pachylemur insignis* suggest that it ate mostly fruit and some leaves.

morphology from the living brown and ring-tailed lemurs, similar to those between the ruffed lemurs and the other genera. In *Pachylemur*, the talonid basin (a basin at the back end of the lower molars) is more elongate, and it is not lined by an entoconid cusp. In the first two upper molars, the lingual cingulum (a shelf on the inner, or lingual, side of the tooth) is expanded towards the front.^[3] The two species differ in details of tooth morphology. *P. insignis* had narrower lower premolars and molars, and the buccal (outer) cusps on these teeth are located to the front of their lingual counterparts.^[4] Relative to the ruffed lemurs, *Pachylemur* has more massive jaws and larger molars.^[3]

The skull of *Pachylemur* is relatively broad, but the orbits (eye sockets) are smaller and oriented more towards the front than in the ruffed lemurs.^{[3][4]} In the postcranial skeleton, the most distinctive traits of *Pachylemur* are found. It had shorter and more robust limbs than the ruffed lemurs, and the fore- and hindlimbs were closer in length (intermembral index of approximately 97).^[4]

Compared to the axial skeleton of ruffed lemurs, the vertebrae of *Pachylemur* had shorter vertebral bodies and the spinous process had less anticlinal. The head of its femur (thigh bone) was also relatively large.^[29] As of 2001, no bones of the digits had been found for either species.^[30]

Behavior

Based on dental wear and the presence of dental caries,^{[31][32]} *Pachylemur* was likely a fruit specialist, just like the closely related ruffed lemurs,^{[31][33][34]} but unlike most of the other leaf-eating, extinct, giant lemurs of Madagascar.^[32] Although it primarily ate fruit, it may have supplemented its diet with leaves and other foliage seasonally.^[35] Its teeth were similar in appearance to that of ruffed lemurs, while its molars and uneven dental wear suggest that it ate fewer leaves and more hard fruits and stems than today's brown lemur species.^[31]



Baobabs in the Madagascar spiny thickets may have once relied on *Pachylemur* to distribute its large seeds.

Because it ate larger, harder, more fibrous fruits than ruffed lemurs,^[36] *Pachylemur* was likely an important seed disperser compared to the more folivorous extinct giant lemurs.^[31] Within the spiny thickets of southwest Madagascar, only *P. insignis* and *Archaeolemur majori*, a type of extinct monkey lemur, are suspected of having been large-seed dispersers, particularly for plants that use a form of photosynthesis known as C₃ carbon fixation.^[37] The plants that may have depended on these giant extinct lemurs include *Adansonia* (baobabs), *Cedrelopsis*, *Commiphora*, *Delonix*, *Diospyros*, *Grewia*, *Pachypodium*, *Salvadora*, *Strychnos*, *Tamarindus*, and *Uncarina*.^[38]

Black-and-white ruffed lemurs can swallow seeds with a diameter up to 30 millimeters (1.2 in), which is larger than any other living lemur. Having been more than twice as large, *Pachylemur* would have been capable of swallowing even larger seeds.^[39] In the case of baobabs,

the fruits have large seeds surrounded by a nutritious pulp and may have required seed dispersal through ingestion.^[38] In western Madagascar, the genetic diversity of *Commiphora guillaminii* suggests it had more widespread seed dispersal in the past, but today shows signs of more localized diversity when compared to African species within the same genus that have not lost their seed dispersers.^[39]

Many small trees and shrubs in the spiny thickets, such as endemic *Uncarina*, conserve water by producing seeds with hooks and spines rather than fleshy fruits. These seeds attach themselves to the skin and fur of passing animals for dispersal, and are still dispersed by living lemur species as well as introduced species such as cattle. *Pachylemur* may also have helped disperse seeds in this fashion.^[40]



Pachylemur may have spread seeds of plants like *Uncarina roeoesliana* by carrying them on their fur.

For many years, palaeoanthropologists thought that *Pachylemur* was a ground-dwelling lemur due to its robust postcranial skeleton.^[2] Yet more recent analysis of its axial and appendicular skeleton—particularly the vertebrae and femur—suggests that it was a tree-dweller (arboreal).^{[2][29]} Like the ruffed lemurs, *Pachylemur* was also an arboreal quadruped that frequently exhibited hindlimb suspension in order to reach fruit and leaves on smaller branches. However, *Pachylemur* was a slow, deliberate climber unlike the ruffed lemurs, which leap and bound through the upper canopy.^{[41][42]} Like the both living lemurs and extinct lemurs, *Pachylemur* likely conserved energy because of its diet, small brain, and slow climbing.^[33]

Because its eyes were comparable in size to those of modern day-living (diurnal) lemurs, *Pachylemur* was probably diurnal as well, as were most of the giant, extinct lemurs. However, compared to similarly sized anthropoid primates, its visual acuity was relatively poor.^[43]

Distribution and habitat

The subfossil remains of *Pachylemur* have been found in all regions of Madagascar,^[44] except in the eastern rainforests where no subfossil sites are known.^[45] The two species are typically found in the spiny thickets and succulent woodlands of southern/southwestern Madagascar (*P. insignis*) and the subhumid forests of the central highlands (*P. jullyi*), although other indeterminate or fragmentary remains have been discovered at Ankilitelô Cave in southwestern Madagascar,^[46] as well as in the dry deciduous forests at Amparihingidro in the northwest (possibly *P. insignis*) and Ankarana in the northern tip of the island (possibly *P. jullyi*).^[47]

Subfossil sites with *P. insignis* include Andolononby,^[48] Beloha (near Anavoha), Bemafandry, Andrahomana, Manombo-Toliara, Ambolisatra, Ambararata-Mahabo, Ampoza-Ankazoabo, Belo-sur-mer, Lamboharana, Taolambiby, Tsiandroina, and Tsirave in south and southwestern Madagascar.^[1] *P. jullyi* has been recorded at Ampasambazimba, Antsirabe, and Morarano-Betafo in the central highlands of Madagascar.^[1]

In general, lemur diversity has declined since the arrival of humans due to habitat loss, forest fragmentation, and bushmeat hunting. At some subfossil sites, *Pachylemur* lived alongside as many as 19 or 20 other lemur species, but now as few as 20% of those species remain in those areas.^[49]

Extinction

Humans arrived in Madagascar around 350 BCE, but did not cause the extinction of *Pachylemur* and the other giant lemurs immediately. Instead, many human-related factors, such as habitat loss, forest fragmentation, bushmeat hunting, and the introduction of invasive species, along with the gradual desiccation of certain parts of the island, caused their decline and eventual extinction over more than a millennium.^[50] The same factors threaten all living lemur species today.^[51]

The initial decline of *Pachylemur* began within 500 years of human colonization, but prior to the establishment of large human settlements. Hunting in the Central Highlands and the spiny thickets likely caused a substantial drop in its population.^[51] Large lemurs, including *Pachylemur*, survived in the Central Highlands, succulent woodlands, and spiny thickets until around 950 CE.^{[51][52]} Based on radiocarbon dating of subfossil remains collected as of 2010, the most recent remains of *P. insignis* out of 17 dated specimens came from Ankilibehandry in the succulent woodlands and dated between 680 and 780 CE. Of eight dated specimens, the most recent remains of *P. julayi* came from Ampasambazimba in the Central Highlands and dated between 620 and 680 CE.^[53] *Pachylemur* is generally thought to have gone extinct between 680–960 CE,^[47] but remains of *P. insignis* have been found in Ankilitelo Cave (a pit cave in southwestern Madagascar), which is assumed to be less than 500 years old.^[54]



Two *P. insignis* skulls, Musee d'Histoire Naturelle, Paris

Notes

- a. Spelling corrected by Zijlstra, Groves & Dunkel 2011, p. 276.

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3. Godfrey & Jungers 2002, p. 114.
4. Godfrey, Jungers & Burney 2010, p. 361.
5. Crovella et al. 1994, p. 519.
6. Godfrey, Jungers & Schwartz 2006, p. 43.
7. Filhol 1895, p. 12.
8. Grandidier 1899, p. 345.
9. Smith 1903, p. 337.
10. Grandidier 1905, p. 78.
11. Pastorini, Forstner & Martin 2002, p. 471.
12. Yoder & Irwin 1999, p. 358.
13. Standing 1904, p. 306.
14. Standing 1904, p. 309.
15. Standing 1904, p. 305.
16. Standing 1908, p. 119.
17. Standing 1908, p. 121.
18. Lamberton 1948, p. 7.
19. Zijlstra, Groves & Dunkel 2011, p. 277.
20. Godfrey & Jungers 2002, p. 105.
21. Tattersall 1982, pp. 240–241.
22. Zijlstra, Groves & Dunkel 2011.
23. Filhol 1874, p. 18.
24. Zijlstra, Groves & Dunkel 2011, pp. 275–276.
25. Zijlstra, Groves & Dunkel 2011, pp. 276–277.

26. Zijlstra, Groves & Dunkel 2011, p. 275.
27. Zijlstra, Groves & Dunkel 2011, p. 278.
28. Godfrey & Jungers 2002, p. 106, table 7.1.
29. Jungers et al. 2001, pp. 391–392.
30. Jungers et al. 2001, p. 394.
31. Godfrey, Jungers & Burney 2010, pp. 361–362.
32. Godfrey, Jungers & Schwartz 2006, p. 50.
33. Godfrey, Jungers & Schwartz 2006, p. 57.
34. Godfrey & Jungers 2003, p. 1249.
35. Jungers et al. 2001, p. 387.
36. Nowak 1999, p. 77.
37. Crowley, Godfrey & Irwin 2011, p. 31.
38. Crowley, Godfrey & Irwin 2011, p. 33.
39. Crowley, Godfrey & Irwin 2011, p. 34.
40. Crowley, Godfrey & Irwin 2011, pp. 33–34.
41. Godfrey & Jungers 2003, p. 1248.
42. Simons 1997, p. 148.
43. Godfrey, Jungers & Schwartz 2006, p. 53.
44. Godfrey et al. 1997, p. 236.
45. Godfrey & Jungers 2002, p. 117.
46. Muldoon 2010, p. 343.
47. Godfrey, Jungers & Burney 2010, p. 354, 361.
48. Crowley, Godfrey & Irwin 2011, p. 28.
49. Godfrey & Jungers 2002, pp. 117–118.
50. Godfrey, Jungers & Burney 2010, p. 363.
51. Crowley 2010, p. 2601.
52. Burney et al. 2004, p. 38.
53. Crowley 2010, Supp. data.
54. Godfrey & Rasoazanabary 2011, p. 171–172.

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